

ECOLOGICAL STUDIES IN A SCANIAN WOODLAND AND MEADOW AREA, SOUTHERN SWEDEN

IV. GRADIENT ANALYSIS OF VEGETATIONAL AND ENVIRONMENTAL PATTERNS

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IV. Gradient analysis of vegetational and environmental
patterns

by Folke Andersson* and Ewa Kvillner +

* Swedish Coniferous Forest Project, the Swedish University
of Agriculture Sciences, Uppsala, Sweden, and

+ Department of Plant Ecology, University of Lund, Sweden.

ABSTRACT

Principal components analysis (R-technique) was used to study the vegetational and environmental structure in a deciduous woodland and meadow area in southern Sweden. Comparison between numerical and non-numerical gradient analysis showed that the distribution of loadings of species along the first principal vegetation axes, accounting for 47% of the total variance, was similar to that on the vegetational gradient "low herb-tall herb", while the first principal axes of environmental data, accounting for 81% of the total variance, revealed that the total effect of soil moisture, acid-base status, exchangeable cations, organic matter and soil structure made a further interpretation of the environmental gradient "dry-wet". Simple correlations with environmental variables explained most of the vegetational variation. Canonical correlation analysis was used to directly relate the vegetation to the environment.

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The data sampling was planned and carried out by Andersson, who also was responsible for the non-numerical gradient analysis. The numerical gradient analysis was planned and carried out by Kvillner, who also was responsible of all data processing. The authors are jointly responsible for the discussion.

1 INTRODUCTION

During 1960-62 an intensive study of the deciduous woodland and meadow area, Linnebjerg, Scania, southern Sweden, was made (Andersson 1970). Vegetational and environmental structures were particularly carefully investigated. A non-numerical gradient analysis method was used in order to relate different soil-water regimes in terms of a "dry-wet" gradient to the differentiation of the vegetation. The vegetation, mainly the field layer, was described by floristic, sociological and ecological groups. A good agreement was found between the different groups of species or types of plant and position along the gradient.

At the time of publication of the work, numerical methods for classification and ordination of vegetational and environmental patterns were developing rapidly. The senior author started at that time to apply some numerical methods. The junior author has used the Linnebjerg material to test a number of numerical methods.

In this paper, the variation of vegetation and environment is analyzed with principal components analysis, PCA. In order to relate vegetation and environment to each other, simple correlations as well as canonical correlation analysis is used. The result of the numerical analyses is then compared with the previously obtained result from the non-numerical analyses.

The original non-numerical analysis (Andersson 1970) was discussed in terms of a "dry-wet" gradient, but now additional environmental variables have been included in the numerical gradient analysis.

2 THE INVESTIGATION AREA

The Linnebjerg wood, seven km ENE of Lund, is a Nature Reserve with an area of 23 ha. It is within the nemoral zone. The bedrock, Silurian slate, is covered with a thin layer of moraine clay. The area slopes towards the North and a characteristic microtopographical variation is found, due to shallow depressions. This topographic variation is also reflected in the ground water table. The depressions have higher ground water levels compared to the surrounding parts. The depressions are occupied by tall herb meadows, grass-lowsedge fens and a magno-caricion fen. The main part of the woodland is covered by a multilayered forest with an overstorey of oak (*Quercus robur*) and linden (*Tilia cordata*) and an understorey of hazel (*Corylus avellana*). The field layer of the woodland also indicates a variation from dry to wet conditions. This differentiation into woodland and meadow has been summarized in a vegetational gradient with a "low herb-tall herb" gradient and a "tall herb-sedge" gradient. A summary of vegetational and environmental conditions is given in Table 1.

3 MATERIAL AND METHODS

3.1 Material

Vegetational data for the gradient analysis were collected from a selected area 130 x 140 m, typical of the whole, which was divided into 10 x 10 m squares, giving a total of 182 squares (see Andersson 1970, Fig. 5 and 10).

Environmental variables were derived from soil samples collected from the centre in 97 of the 182 10 x 10 m squares in eight transects, which were subjectively chosen out of the fourteen available transects.

In the following text two types of material will be discussed:

- The 182-material = including notations of species frequency in the 182 10 x 10 m squares.
- The 97-material = including notations of both vegetational and environmental data in the 97 10 x 10 m squares.

3.2 Methods

3.2.1 Non-numerical methods

3.2.1.1 Vegetation

All plants were recorded for presence in 2.5 x 2.5 m subsquares. Distribution maps were made for species in a sociological analysis with the frequency value >25%, giving 63 species. However, one species, Carex Hartmanii, was not mapped, thus giving a total of 62 species (Andersson op cit. Fig. 11 and Appendix Figs 3-63). Maps were also made for some species of low frequency, but with high diagnostic value. Bryophytes were not

mapped. Maps with a similar distribution type were sorted into different floristic groups.

For each species the percentages of 10 x 10 m squares in which it occurred associated with a particular soil water regime was calculated. The percentages of occurrence were grouped in the following classes: 100-75, 75-50, 50-25, 25-13 and 13-5. Percentages <5% were disregarded. From this material ecological groups were established.

3.2.1.2 Environment

A detailed study of ground water regimes and distribution of soil types had already been made (Andersson op.cit. p. 135-142). The map of the soil types was derived from more than 200 descriptions of soil cores and soil profiles in the selected area. The ground water regimes were defined by median water level, duration of characteristic water level and soil aeration.

On the 97 soil samples the following analyses were made:

Dry bulk density (g.cm^{-3})=Bulk	N-total (g.dm^{-3})=N-tot
Actual soil water content	Exchangeable P (mmol.dm^{-3})=P
(%)=Water	
Loss on ignition (% d.wt.)=Loss i	Exchangeable K (mmol.dm^{-3})=K
pH_{KCl}	Exchangeable Ca (mmol.dm^{-3})=Ca
$\text{pH}_{\text{H}_2\text{O}}$	Exchangeable Mg (mmol.dm^{-3})=Mg
Base saturation (%)=Base sat	Exchangeable H (mmol.dm^{-3})=H
Cation exchange capacity	Exchangeable Na (mmol.dm^{-3})=Na
($\text{meq} \cdot \text{dm}^{-3}$)=Cat exch	

3.2.2 Numerical methods

Ordination of the Linnebjerg material was carried out by PCA, a method which for a long time has been applied to biological data, especially to vegetational patterns (indirect gradient analysis by Whittaker 1967, see e.g. Goodall 1953, Dagnelie

1960, Groenewoud 1965, Austin and Orloci 1966, Gittins 1968, Goff 1975). PCA has also been used to analyze environmental patterns by e.g. Barkham and Norris (1970). The method is a generally useful ordination procedure whenever the task is to determine the minimum number of independent components/ gradients needed to account for most of the variance in the original set of variables. The PCA-ordination is most useful when applied to a narrow range of ecological gradients (Greig-Smith 1964, Whittaker 1967). The method is based upon assumptions on linearity (see e.g. Whittaker 1967, Swan 1970), which has raised some objections to its applicability to vegetational data.

The present PCA-analysis started from each of the three unstructured data matrices, i.e. the vegetation data matrices 182×62 and 97×62 , and in addition the environment data matrix 97×14 . Covariance coefficients were calculated between frequency values of all possible pairs of species. The frequency was based on the presence of species in $16 \times 2.5 \times 2.5$ m subsquares in each 10×10 m square. Correlation coefficients were used to compute the relationships between all pairs of environmental variables. Three matrices were consequently made, transforming the original data matrices to two 62×62 covariance matrices and one 14×14 correlation matrix. Each of these latter matrices was used in further calculations to express the observed variables (species or environmental variables) in terms of hypothetical non-observed new variables (components or axes). The next step was an estimation of loadings (also called latent vectors or eigenvectors), i.e. the coordinates of observed variables on the components. Simultaneously an estimation of variances (also called latent roots, eigenvalues or communalities) was made, i.e. the sums of squares of loadings, measuring the importance of each component and the importance of these components for each observed variable. Finally, rotation of axes was carried out to get more meaningful axes. The result was presented in a rotated factor matrix. The observed variables can be divided into two

different types according to the distribution of their loadings on the principal axes, viz.:

- A) Variables with a high loading (positive or negative) on one axis only and
- B) Variables with high loadings on more than one axis.

In this connection the coefficients of the stands or stand scores on the principal axes were also computed.

The relationship between the vegetation and the environment is here tested by two different methods (see Austin 1968, Barkham and Norris 1970, Dagnelie 1971). Firstly, the values of each environmental variable were plotted against stand scores on each principal axis. The relationship was tested by a simple correlation. Secondly, the two sets of variables were combined to make maximum correlation between the variables. This was done by canonical correlation analysis.

In the simple correlations of the environmental variables with the principal vegetation axes, correlation coefficients were calculated and significant relationships were reported. In the canonical correlation analysis, the correlation coefficients were calculated between all pairs of variables. The correlation matrix was used to obtain canonical variables or vectors of each set of variables. The loadings of these vectors are the correlations of the original variables with the canonical variables. To obtain maximum correlations with the canonical variables of each set, canonical correlations (i.e. the squares roots of the eigenvalues) were calculated. A special χ^2 -test (Barlett's test, see Cooley and Lohnes 1962) was used to locate significant combinations.

In carrying out the analyses, the UNIVAC 1103 computer of the University of Lund was used. The PCA analysis was done with the standard programs BMD X72 and BMDP P4M. The canonical correlation analysis was computed with the standard program BMDP P6M.

4 RESULTS

4.1 Non-numerical gradient analysis

As a background to the interpretation of the numerical gradient analysis, a summary of the main results of the non-numerical analysis is given. For details, see Andersson 1970.

4.1.1 Vegetation

The distribution maps and the sociological analysis revealed floristic and sociological groups showing great resemblances. From this material and an interpretation of the life forms, vegetational gradients were established. The variation could be described along two gradients: the "low herb-tall herb" gradient and the "tall herb-sedge" gradient. The former represents the variation from dry to moist woodland and the latter from moist to wet open meadows and fen.

4.1.2 Environment

Fig. 1 shows the distribution of ecological groups on soil-water regimes. Group 1 and 2 represents woodland species with moderately dry to fresh soil water conditions with a median water level of 2-6 dm and aeration of the upper 50 cm of the soil during most of the year. Group 3 is woodland species occurring from moderately dry to moist conditions with medium water level of 1-6 dm. Group 4 contains indifferent species, mostly meadow plants. Group 5 consists of meadow species with occurrence in the tall herb meadow as well as in the fen. Group 6 finally, contains species with moist and wet water regimes prevailing in the grass-lowsedge meadow. The wet soil water regime has a medium water level <1 dm and range of 2-5 dm. In the magnocaricion fen, the Carex caespitosa-community, high water levels show longer duration than in the grass-lowsedge meadow. There is also

a tendency towards impaired aeration affecting especially the biological processes in the soil, in particular the nitrogen turnover.

The "dry-wet" gradient is correlated with a soil chemical gradient from acid to basic conditions. This can be demonstrated with the acid-base status of the soil in terms of pH, base saturation, cation exchange capacity or the distribution of exchangeable hydrogen and calcium (c.f. Table 1).

4.2 Numerical gradient analysis

4.2.1 Vegetation

The most abundant species were found in the non-numerically identified ecological groups 2 and 3, which together with group 1 correspond to woodland species (Table 2). Most of the meadow species, i.e. groups 5 and 6, were infrequent.

The distribution of loadings of species in the "182"-material was found to be very similar to that of the "97"-material. This is further discussed in Kvillner (1977). The first three principal axes, accounting for 55 and 56% of the total variance respectively, were chosen for interpretation of the vegetational structure. The extracted variance and the distribution of loadings of species in the two sets was very similar and provides a good basis for choosing the "97"-material to represent the vegetation of the area, thus making it possible to compare the vegetational and environmental structure on the same sampling area. The distribution of stand scores on the first three principal axes in the "97"-vegetation material is shown in Fig. 6a.

High negative loadings on the first principal vegetation axis (axis 1 in Figs. 2 and 4), representing 33% of the total variance, were found for species belonging to group 2

and 2b, e.g. Anemone nemorosa, Convallaria majalis and Oxalis acetosella. The loadings of the remaining part of the species of group 2 were distributed mainly along the negative part of the first axis towards the origin, e.g. Rubus saxatilis, Hypericum perforatum, Melampyrum pratense and Lactuca muralis. The two species of group 1 were positioned near the origin together with species of group 4, e.g. Prunella vulgaris, Potentilla erecta, Succisa pratensis, Serratula tinctoria, and the species of group 6, e.g. Carex panicea, Eleocharis uniglumis and Carex flacca. High positive loadings were found for species belonging to group 3b, e.g. Ranunculus auricomus, Crepis paludosa, Geum rivale, and group 5b, e.g. Filipendula ulmaria, Caltha palustris, Lysimachia vulgaris, Myosotis palustris. Consequently, the first principal axis primarily showed the great variation within the distribution of loadings of woodland species (along the whole of the axis) but also a variation within the distribution of loadings of meadow species (along the positive part of axis 1).

On the second principal vegetation axis (axis 2 in Figs. 2 and 3) which accounted for 13% of the total variance, high positive loadings were found for Deschampsia caespitosa and Anthriscus sylvestris belonging to group 3b, and for Fragaria vesca, Melandrium rubrum, Veronica chamaedrys, Lathyrus montanus and Viola riviniana coll. belonging to group 2 and 2b. The loadings of the remaining species belonging to these groups were distributed mainly along the positive part of the axis, while the negative part of the axis was developed mainly by species of group 5b. The species of group 6 were found near the origin. Again the greatest variation was found within the distribution of loadings of woodland species along most of the second principal axis.

The third principal vegetation axis (axis 3 in Figs. 3 and 4) accounted for 11% of the total variance. The species of group 4, e.g. Achillea ptarmica, together with the species of group 5 and 5b, e.g. Lychnis flos-cuculi, Equisetum arvense, Holcus lanatus, and the species of group 6, e.g.

Juncus conglomeratus, Eleocharis uniglumis, Eriophorum angustifolium and Briza media, accounted for the development of the negative part of the third axis, while the loadings of species of group 3 and 2 were mainly found at the positive part. Thus a fairly weak division of the third axis into woodland and meadow species was distinguished.

4.2.2 Environment

Some of the 14 environmental variables were highly inter-correlated. The highest correlations ($r > 0.90$) were found between $\text{pH}_{\text{H}_2\text{O}}$, pH_{KCl} , base saturation, cation exchange capacity and exchangeable calcium (Table 3).

The first three axes of PCA-ordination of environmental data accounted for 62, 11 and 8% of the total variance respectively. The distribution of stand scores on the axes is shown in Fig. 6b. Several variables had high loadings on the first principal environment axis (Table 4 and Fig. 5). At the positive end pH, base saturation, cation exchange capacity, exchangeable calcium, magnesium and sodium as well as actual soil water content were most highly loaded, at the negative end exchangeable hydrogen was most significant, thus summarizing the first axis to the total effect of acid-base status including the stores of exchangeable cations and soil moisture in the area. These variables (A-variables, see p.7) together contributed 86% of the variance (sum of eigenvalues = 7.46) accounted for by the first axis and 57% of the total variance (sum of h^2 -values = 7.93) accounted for by all three axes.

The second principal environment axis showed positive loadings of loss on ignition and total nitrogen and a high negative loading of dry bulk density, which indicated the effect of organic matter and soil structure on that axis. These variables (B-variables) contributed 96% of the variance (sum of eigenvalues = 1.46) accounted for by the

second axis, but also 10% of the variance (sum of eigenvalues = 0.85) represented by the first axis and 17% of the total variance (sum of h^2 -values = 3.34) accounted for by all three axes.

Exchangeable phosphorus and potassium (A-variables) contributed 77% of the variance (sum of eigenvalues = 0.90) accounted for by the third principal environment axis and 7% of the total variance (sum of h^2 -values = 1.02) accounted for by all three axes.

4.3 Linking of vegetation and environment

The correlations between the environmental variables and the distribution of stand scores along the three principal vegetation axes are given in Table 5. Most of the environmental variables were related to the first axis. Thus pH_{H_2O} ($r = 0.77$), pH_{KCl} ($r = 0.76$), exchangeable hydrogen ($r = -0.70$) and calcium ($r = 0.70$), base saturation ($r = 0.74$), cation exchange capacity ($r = 0.69$), actual soil water content ($r = 0.71$), exchangeable magnesium ($r = 0.65$) and sodium ($r = 0.58$) as well as loss on ignition ($r = 0.52$) showed high correlations at the 0.1% significance level. Significant correlations were also shown by total nitrogen ($r = 0.30$) and exchangeable potassium ($r = 0.26$). Along the first principal vegetation axis a gradient towards a neutral soil reaction, great reserves of exchangeable base cations and high soil moisture is demonstrated. The second principal vegetation axis is significantly correlated only with dry bulk density ($r = 0.38$), relating the axis to gradual changes in soil structure. The third principal vegetation axis was correlated with loss on ignition ($r = -0.46$), actual soil water content ($r = -0.39$), total nitrogen ($r = -0.29$) and exchangeable potassium ($r = -0.23$). The correlations of environmental variables with the second and third principal vegetation axes were thus not high, though significant.

By canonical correlation analysis the sets of species and environmental variables can be combined in at least five different ways at the 1% significance level with canonical correlations of 0.99, 0.96, 0.95, 0.92 and 0.90 respectively (Table 7). The infrequent species Potentilla erecta, Serratula tinctoria, Molinea coerulea, Selinum carvifolia, Eleocharis uniglumis, Dactylorhiza majalis and Eriophorum angustifolium were excluded in the analysis as well as cation exchange capacity, thus decreasing the number of variables to 55 species and 13 environmental variables. The contributions made by the different variables to the vectors of each canonical correlation are given in Table 6. The positive loadings revealed the most significant relationship to be between meadow species of groups 5b, 5 and 6 as well as woodland species of group 3b, and soil water content, pH, base saturation, loss on ignition, exchangeable calcium, magnesium and sodium as well as total nitrogen. Negative loadings were found for woodland species belonging to groups 2 and 2b and for exchangeable hydrogen. The second canonical correlation was composed of vectors with positive loadings for a mixture of some woodland and meadow species of the groups 3, 2, 1, 4, 5b and for exchangeable calcium, base saturation, pH, dry bulk density. The loadings were however not high. The third canonical correlation related woodland species of groups 2 and 3 to dry bulk density, exchangeable magnesium and sodium, base saturation, pH and exchangeable calcium. The fourth canonical correlation showed the relationship between some woodland species of group 2 and dry bulk density and exchangeable potassium. The fifth canonical correlation was composed of negative loadings for species belonging to group 3, 3b, 5, 6 and 2 and positive loadings for exchangeable potassium and total nitrogen.

5 DISCUSSION

The main vegetational pattern visible in the Linnebjerg area is the differentiation into woodland and meadow. This vegetational gradient, earlier distinguished as a "low herb-tall herb" gradient, is found along the first principal vegetation axis as transitional changes in the distribution of loadings of species from low woodland herbs (groups 2 and 2b) towards tall woodland herbs (groups 3 and 3b) and tall meadow herbs (groups 5 and 5b). The greatest part of the variation is consequently shown within the distribution of loadings of woodland species which in the numerical gradient analysis ranged the whole of the first axis, accounting for 33% of the total variance in the data (Fig. 2 and 4).

Some part of this variation is however partly due to the number of very frequent and common woodland species, i.e. the woodland species tend to be "overrepresented" in comparison with the meadow species, when covariance matrix is used since high covariance is found between two species only when both are relatively common and when they display the same phytosociological pattern. This also means that in a covariance matrix, a species contributes in proportion to its variance (c.f. Noy-Meir 1973, Noy-Meir, Walker and Williams 1975, Goff 1975, Kvillner 1977). Yet the distribution of loadings of species also emphasizes the wide amplitudes of the woodland species, also shown in the non-numerical gradient analysis, where the distribution of species ranged over three quarters of the "dry-wet" gradient from moderately dry towards fresh and moist soil-water regimes. It should be noted however that the second principal vegetation axis scarcely contributes to a further explanation of the variation, but a widespread of loadings is obtained.

However, a large-scale gradient, like the "low herb-tall herb" gradient, is distorted by the numerical gradient ana-

lysis, because of the implicit linearity assumed between vegetation and environmental gradients in the PCA-ordination (c.f. Whittaker 1967, Swan 1970, Kvillner 1977). This means that it may conceal other important directions of variation visible in the field. Thus the narrow "tall herb-sedge" gradient, visible in the open meadow vegetation, is but partly distinguished in the PCA-ordination. Neither does the third principal vegetation axis contribute to this variation.

In the environmental system, a clearly distinguished "dry-wet" gradient is visible in the field, primarily due to the microtopographical variation in the area. Other variables, e.g. soil aeration, were correlated in the gradient which was manifest in the soil types and the humus types. A chemical gradient from acid to basic conditions also followed the non-numerically described "dry-wet" gradient. This gradient is further elucidated in the numerical analysis in terms of the relationship between soil water content and other environmental variables measured. Especially significant is its relationship with the acid-base status in terms of pH, base saturation, cation exchange capacity and exchangeable calcium and hydrogen. Some exchangeable base cations (sodium and magnesium) also take part in this variation. Thus a "dry-wet" gradient is established by numerical methods in terms of primary environmental variables i.e. soil moisture, acid-base status and, perhaps least important, some exchangeable base cations. These variables account for most of the total variance in the environment data. It should be noted however that, in the numerical analysis, the soil water complex is represented by one single variable, while there is a large number of variables included in the acid-base status.

Secondary environmental variables, i.e. organic components (loss on ignition and total nitrogen) and soil structure, form a connection between the first and the second principal

environment axes. These axes are consequently not independent of each other. Exchangeable potassium and phosphorus, though ecologically important, were proved to be of least importance in the numerical analysis, accounting for the third principal environmental axis.

Gradual changes in the environment were previously described as the variation along an environmental gradient, which - composed of a number of associated variables - relate to quantitative changes in the species composition within the area. The vegetational and environmental gradients were linked together by thorough comparison of spatially distributed patterns.

The corresponding gradients were found numerically though with somewhat different variables. No straight linear relationship between the gradients was expected, since both were found to be distorted in the PCA-ordination. Almost the same picture, given by the principal environment axes, is found by linking the environment to the vegetation by simple correlations. Thus most of the variation along the numerical "low herb-tall herb" gradient is related to transitional changes of variables in the "dry-wet" gradient. Further, by the first canonical correlation, the vegetational vector, ranging from low woodland herbs (group 2 and 2b) towards tall woodland herbs (group 3b) and tall meadow herbs (group 5 and 5b), is related to the environmental vector, ordering the variables into soil water content, acid-base status, exchangeable base cations and organic matter. By this linking method, the species of group 6 (as well as those of group 4) have a proportionally greater significance. This depends upon the use of a correlation matrix, in which the contributions of all variables (infrequent as well as frequent species) are equalized (see Noy-Meir 1973, Noy-Meir, Walker and Williams 1975, Kvillner 1977). It also gives a slight indication of the "tall herb-sedge" gradient, though in a rather incomplete way. Nevertheless, it seems likely that the remaining canonical correlations, though representing interesting

combinations of species and environmental variables, are more statistically than ecologically significant. Unfortunately, the analysis did not comprise an analysis of nitrogen fractions connected with biological activity, which could have given a better ecological interpretation.

However, some environmental variables expected to have a high diagnostic value, e.g. exchangeable phosphorus and potassium, as well as some species, indicating the terminal points of the original environmental gradient i.e. species belonging to group 1 and 6, did not turn out to be significantly important in any of the numerical methods used. Instead, a simplified numerical "low herb-tall herb" gradient, emphasizing the wide amplitudes of woodland species, was related to a composed "dry-wet" gradient with strong connections with the acid-base status. Nevertheless, the ecological group 1, consisting of only two species viz. Poa nemoralis and Carex montana, is too small to achieve importance in any numerical method, while an ecologist, using a variety of information from other sites would consider the group of diagnostic value.

Unfortunately, light was not included as a variable in the analysis. It might be expected for good reasons that it could have further emphasized the variation from woodland to meadow. A numerical classification procedure, dividing the large-scale gradient into woodland and meadow, followed by ordinations of the separate units, might also have given an interpretation of the hidden variation along the "tall herb-sedge" gradient.

The non-numerical and numerical gradient analyses give similar results. However, absence of a species as well as an environmental variable with a high diagnostic value will affect the numerical analysis more than the non-numerical analysis. The observations in the field as they are expressed in the non-numerical descriptions form a hypothesis

about the relation between the vegetational and environmental features. The numerical analysis was then used to test the hypothesis. Obvious similarities have been found in the results and to a great extent it is validated. The numerical analysis also suggested further hypotheses. It must however be stressed that statistical methods should be used with care in tracing ecological relationships: they are no substitute for experimental evidence. The same of course is true of non-numerical methods.

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Table 1. Summary of vegetation and environment of the Linnebjerg Wood.
For further details, see Andersson 1970.

Vegetation type	Humus and soil type	Ground water level (median value in cm)	Loss on ignition (% d. wt.)	Dry bulk density (g.cm ⁻³ d.wt.)	Chemical properties of the humus layer pH _{H₂O} Base saturation (%)
<u>Woodland - meadow forest</u>					
1. Quercus robur - Oxalis acetosella community	Mull Brown earth semigley	84	15	0.75	4.4 21
2. Quercus robur - Geum rivale community	Mull Eugley	25	18	0.66	6.2 69
3. Quercus robur - Athyrium filix-femina community	Mull-Anmoor Eugley	-	17	-	75
<u>Open meadow and fen</u>					
4. Filipendula ulmaria community - tall herb meadow	Mull Eugley	11	26	0.55	6.5 87
5. Carex flacca - grass sedge meadow	Fenmull Eugley	4	31	0.29	7.0 93
6. Carex caespitosa community - tall sedge fen	Anmoor Wetgley	2	39	0.22	6.9 87

Table 2.

Summary of univariate statistics of vegetational data in the 97- and 182- materials (see text). % occurrence is based upon qualitative vegetation data, mean and standard deviation of species is based on quantitative data. The 62 species are ordered according to ecological groups (Andersson 1970).

Ecological group	Species	Linnebjerg (N=97)		97 - material		Linnebjerg (N=182)		182 - material	
		% Occurrence	Mean	Standard deviation		% Occurrence	Mean	Standard deviation	
1	<i>Poa nemoralis</i>	48.4	19.4	32.91		49.5	19.2	31.78	
	<i>Carex montana</i>	25.8	5.5	13.94		25.3	5.2	13.80	
2	<i>Convallaria majalis</i>	74.2	58.9	44.37		76.4	62.8	42.68	
	<i>Oxalis acetosella</i>	53.8	41.6	45.56		62.1	44.2	45.01	
	<i>Viola riviniana</i> coll.	67.0	29.0	38.97		66.5	32.2	40.88	
	<i>Rubus saxatilis</i>	68.0	26.4	32.75		61.6	25.5	32.45	
	<i>Lactuca muralis</i>	18.6	3.4	9.99		19.3	4.0	12.45	
	<i>Moehringia trinervia</i>	28.9	6.1	17.67		34.7	7.2	18.26	
	<i>Lathyrus montanus</i>	21.6	7.7	19.12		22.0	8.8	21.22	
	<i>Fragaria vesca</i>	57.7	27.7	36.18		60.5	30.6	37.82	
	<i>Hypericum perforatum</i>	12.4	4.2	14.71		13.8	2.9	11.02	
	<i>Melampyrum pratense</i>	21.6	3.3	9.04		20.4	3.3	8.92	
	<i>Veronica chamaedrys</i>	32.0	9.5	22.69		29.2	9.4	22.36	
	<i>Campanula trachelium</i>	14.4	1.6	5.89		11.0	1.5	5.06	
	<i>Anemone nemorosa</i>	93.8	77.4	35.66		91.3	78.4	34.89	
	<i>Epilobium montanum</i>	35.1	6.7	15.79		38.5	7.9	16.87	
	<i>Melandrium rubrum</i>	62.9	26.0	34.97		61.6	24.3	33.25	
3	<i>Geranium robertianum</i>	45.4	12.6	21.83		49.0	14.7	24.73	
	<i>Aegopodium podagraria</i>	63.9	25.4	30.78		60.5	25.7	31.65	
	<i>Ranunculus ficaria</i>	59.8	34.0	36.13		63.2	36.4	37.85	
	<i>Cicarea lutetiana</i>	20.1	2.8	8.77		22.0	3.9	11.28	
	<i>Dactylis glomerata</i>	41.2	11.2	20.79		40.2	12.8	23.84	
	<i>Cirsium heterophyllum</i>	13.4	4.2	14.71		9.9	4.1	15.91	
	<i>Deschampsia caespitosa</i>	75.3	35.5	36.47		73.7	35.4	37.19	
	<i>Anthriscus sylvestris</i>	41.2	13.5	28.86		35.8	11.3	22.99	
	<i>Trollius europaeus</i>	38.1	5.7	10.78		31.9	4.7	9.76	
	<i>Geum rivale</i>	60.8	28.2	36.19		59.9	25.7	33.90	
3b	<i>Crepis paludosa</i>	55.7	23.6	32.99		54.4	23.6	33.41	
	<i>Ranunculus auricomus</i>	62.9	40.4	42.80		65.4	42.1	42.77	
4	<i>Prunella vulgaris</i>	23.7	6.7	17.76		22.6	5.9	16.14	
	<i>Ranunculus repens</i>	54.6	7.9	18.91		55.0	8.1	19.35	
	<i>Achillea ptarmica</i>	24.7	10.5	26.52		20.9	9.0	24.40	
	<i>Potentilla erecta</i>	14.4	3.6	13.88		10.5	2.8	12.62	
	<i>Succisa pratensis</i>	16.5	3.6	13.07		14.9	2.6	10.12	
	<i>Serratula tinctoria</i>	10.3	2.6	12.59		7.2	1.7	9.39	
5	<i>Angelica sylvestris</i>	51.5	16.0	27.55		49.5	16.1	26.66	
	<i>Holcus lanatus</i>	40.2	19.7	34.60		40.2	18.4	33.33	
	<i>Cirsium palustre</i>	34.0	7.4	21.06		29.7	8.2	21.05	
5b	<i>Filipendula ulmaria</i>	41.2	25.0	39.19		33.6	22.8	37.61	
	<i>Geranium palustre</i>	21.6	9.1	22.94		20.9	7.0	19.65	
	<i>Myosotis palustris</i>	32.0	16.9	32.44		31.4	16.8	31.68	
	<i>Lysimachia vulgaris</i>	27.8	16.5	32.61		28.6	15.4	30.99	
	<i>Caltha palustris</i>	20.1	17.8	34.21		18.7	17.0	33.08	
	<i>Carex caespitosa</i>	18.6	11.1	26.42		17.1	9.7	24.68	
	<i>Equisetum arvense</i>	24.7	15.7	31.17		22.0	14.3	30.82	
	<i>Lychnis flos-cuculi</i>	17.5	8.2	23.38		18.2	8.1	22.62	
	<i>Phalaris arundinacea</i>	5.2	2.9	14.47		5.0	2.8	14.34	
	<i>Lythrum salicaria</i>	14.4	1.8	5.08		13.2	1.9	5.66	
	<i>Molinea caerulea</i>	9.2	3.3	13.65		8.3	3.2	12.93	
	<i>Selinum carvifolia</i>	13.4	3.6	13.59		9.4	2.2	10.11	
6	<i>Juncus conglomeratus</i>	14.4	7.4	21.55		13.2	6.2	18.63	
	<i>Carex panicea</i>	9.2	1.4	5.80		7.7	0.9	4.52	
	<i>Eleocharis uniglumis</i>	6.2	3.3	14.72		5.0	2.3	11.52	
	<i>Carex flacca</i>	5.2	3.1	13.44		3.3	2.5	12.41	
	<i>Dactylorchis majalis</i>	7.2	2.3	14.19		5.5	1.3	10.41	
	<i>Briza media</i>	5.2	2.2	11.22		4.4	1.7	9.24	
	<i>Eriophorum angustifolium</i>	5.2	2.0	11.81		3.3	1.2	8.84	
	<i>Epilobium parviflorum</i>	6.2	1.5	8.47		5.5	1.1	6.44	
Unclassified:									
	<i>Mentha</i> sp	10.3	2.1	8.83		34.7	2.5	10.03	
	<i>Poa annua</i>	7.2	2.2	8.06		8.8	2.0	7.25	
	<i>Glyceria fluitans</i>	11.3	1.5	5.18		11.6	1.5	5.04	
	<i>Athyrium filix-femina</i>	20.2	3.8	11.08		19.3	3.5	9.61	

Table 4.

Loadings of habitat variables on the first three principal components (a_1 , a_2 , a_3) of PCA-ordination of correlation matrix, $N=97$. Variance (h^2) is calculated for each habitat variable concerned and for each principal component.

Variable	a_1	a_2	a_3	h^2
pH_{KCl}	0.97	0.02	-0.03	0.94
pH_{H_2O}	0.97	0.02	0.00	0.94
Base saturation	0.96	-0.04	0.03	0.92
Cation exchange capacity	0.95	0.09	0.23	0.96
Ca - exch.	0.95	0.11	0.20	0.95
Mg - exch.	0.93	-0.01	0.28	0.94
H - exch.	-0.87	-0.05	0.11	0.77
Actual water content	0.85	0.26	0.10	0.80
Na - exch.	0.71	0.12	0.44	0.71
Loss on ignition	0.68	0.62	-0.12	0.86
Dry red.bulk density	0.38	-0.78	-0.07	0.76
N-total	0.49	0.68	0.20	0.74
P - exch.	-0.20	0.05	0.72	0.56
K - exch.	0.27	0.05	0.62	0.46
Variance (eigenvalues)	8.63	1.52	1.17	Σ 11.32
As % of total variance (14.00)	61.66	10.82	8.35	80.83
Cummulated	61.66	72.48	80.83	

Table 5.

Relationship between habitat variables and the first three principal axes (component 1, 2 and 3) of PCA-ordination of covariance matrix on vegetation data. Significance at the 5, 1 and 0.1 percent level is denoted with one, two and three asterisks respectively.

Habitat variables	Component 1	Component 2	Component 3
pH _{KCl}	0.756***	-0.020	-0.182
pH _{H₂O}	0.770***	-0.023	-0.088
Base saturation	0.741***	0.019	-0.062
Cation exchange capacity	0.691***	-0.021	-0.082
Ca-exch.	0.704***	-0.018	-0.112
Mg-exch.	0.655***	0.056	0.150
H-exch.	-0.697***	0.074	0.139
Actual water content	0.705***	0.094	-0.391***
Na-exch.	0.581***	0.172	0.054
Loss on ignition	0.524***	-0.163	-0.464***
Dry red.bulk density	0.264*	0.381***	-0.183
N-total	0.296**	-0.069	-0.292**
P-exch.	-0.055	-0.002	0.105
K-exch.	0.257*	0.091	-0.229*

Table 6.

Canonical vectors of the first five canonical correlations of species (n=55) and habitat variables (n=13). Ecological group according to Andersson (1970) is reported for each species. Values between 0.25 and -0.25 are eliminated.

Canonical vectors of canonical correlation 1			Canonical vectors of canonical correlation 2			Canonical vectors of canonical correlation 3		
Ecological group	Species	Habitat variables	Ecological group	Species	Habitat variables	Ecological group	Species	Habitat variables
5b	0.90 Fi.	0.92 Water	3b	0.49 Gr.	0.37 Ca	3	0.55 Ger.	0.53 Bulk
5b	0.78 Eq.	0.90 pH _{KCl}	3	0.36 Raf.	0.36 Base sat.	3	0.54 Raf.	0.52 Mg
5b	0.77 Cal.	0.89 pH _{H₂O}	2	0.33 Cam.	0.30 pH _{KCl}	3b	0.45 Raa.	0.42 Na
5b	0.74 Lys.	0.87 Loss i.	3b	0.26 Raa.	0.26 pH _{H₂O}	3	0.41 Ci.	0.37 Base sat.
5b	0.73 My.	0.84 Ca	1	0.26 Carm.	0.25 Bulk	2	0.41 Moe.	0.32 pH _{H₂O}
6	0.71 J.	0.82 Base sat.	4	0.26 Rar.		2b	0.35 Epm.	0.27 pH _{KCl}
5b	0.70 Lyc.	0.74 Mg	5b	0.26 Cal.		3	0.35 Ae	0.25 Ca
5	0.68 Ho.	0.54 Na	6	-0.32 Carf.		3b	0.33 Gr.	
5	0.60 Cirp.	0.54 N-tot.	2	-0.27 O		3b	0.27 Cr.	
5b	0.58 Carf.	-0.81 H	4	-0.27 Su.		1	-0.29 Pon.	
5b	0.56 Carc.		5b	-0.27 Carc.				
5b	0.55 Lyt.		2	-0.25 Lac.				
4	0.50 Su.		6	-0.25 J.				
3b	0.50 Raa.							
5	0.49 Ang.							
6	0.49 B.							
6	0.46 Carp.							
4	0.44 Ac.							
3b	0.40 Cr.							
3b	0.39 Gr.							
5b	0.38 Ph.							
4	0.37 Pr.							
2b	-0.85 Ane.							
2	-0.69 Co.							
2	-0.53 O.							
2	-0.42 Fr.							
2	-0.39 Ru.							

Canonical vectors of canonical correlation 4			Canonical vectors of canonical correlation 5		
Ecological group	Species	Habitat variables	Ecological group	Species	Habitat variables
2	0.29 Lac.	0.25 Bulk	3b	-0.35 Cr.	0.54 P
2	0.25 Lat.	0.25 K.	5	-0.33 Ang.	0.28 N-tot
			2	-0.33 Lat.	
			3b	-0.30 Ant.	
			3	-0.27 Dg.	
			3b	-0.27 T.	
			2	-0.27 Cam.	
			3b	-0.25 Raa.	
			6	-0.25 Carp.	

Table 7.

Barlett's test of significance of canonical correlations between environmental (n=13) and vegetational (n=55) variables. Barlett's test indicates the number of canonical variables necessary to express the dependence between the two sets of variables. The necessary number of canonical variables is the smallest number of eigenvalues (latent roots) such that the test of the remaining eigenvalues is non-significant.

Number of Roots Removed	Largest Latent Root re- maining	Corresponding Canonical R	χ^2	NDF	P
0	0.936	0.993	1225.3	715	0.000
1	0.920	0.959	964.8	648	0.000
2	0.905	0.951	809.3	583	0.000
3	0.848	0.920	664.7	520	0.000
4	0.801	0.895	549.0	459	0.002
5	0.769	0.877	449.7	400	0.043
6	0.722	0.850	359.7	343	0.257
7	0.678	0.823	281.0	288	0.604
8	0.634	0.796	211.3	235	0.864
9	0.593	0.770	149.5	184	0.971
10	0.563	0.750	94.1	135	0.997
11	0.345	0.588	43.2	88	0.999
12	0.244	0.494	17.2	43	0.999
13	-	-	0	0	1.000

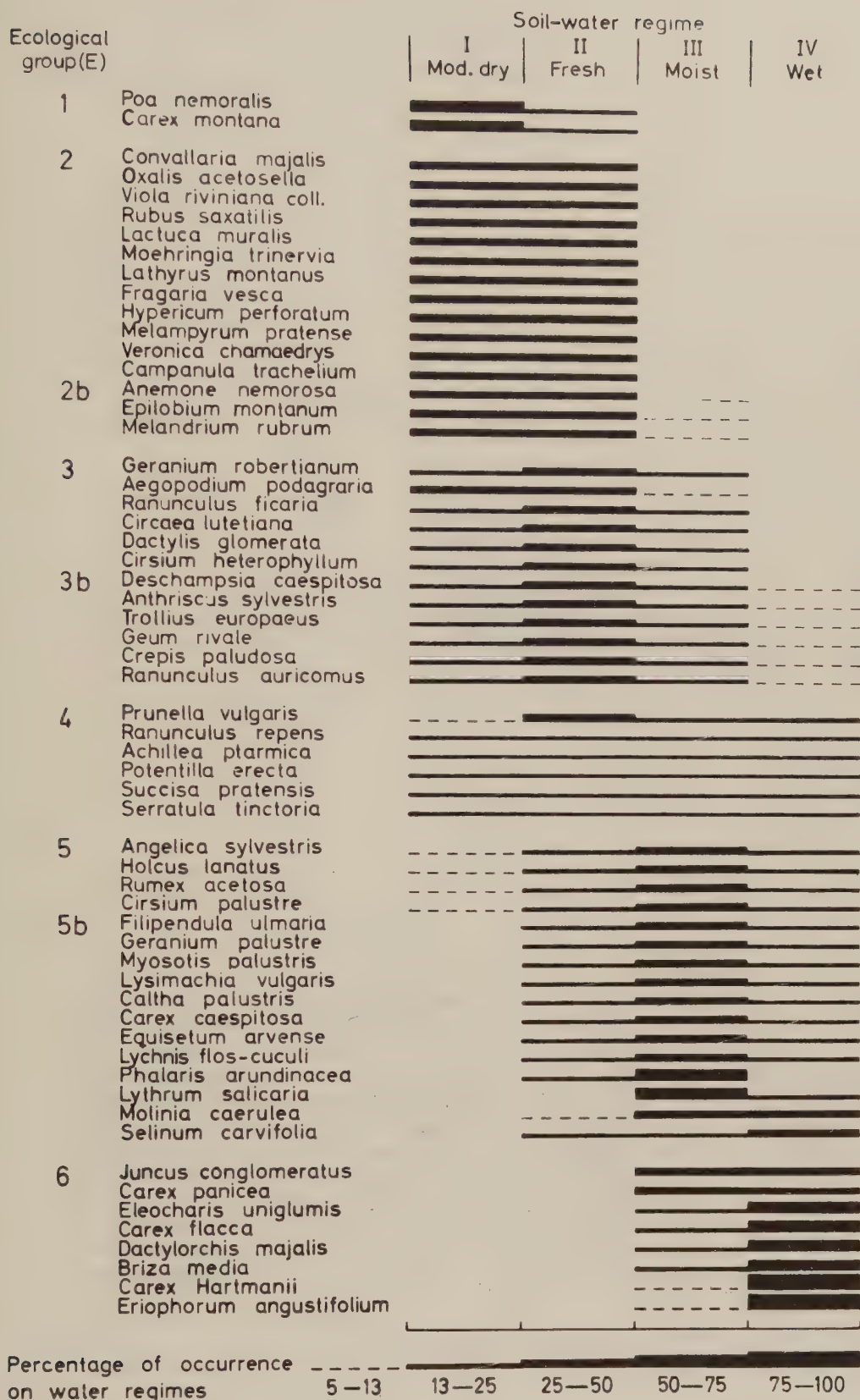
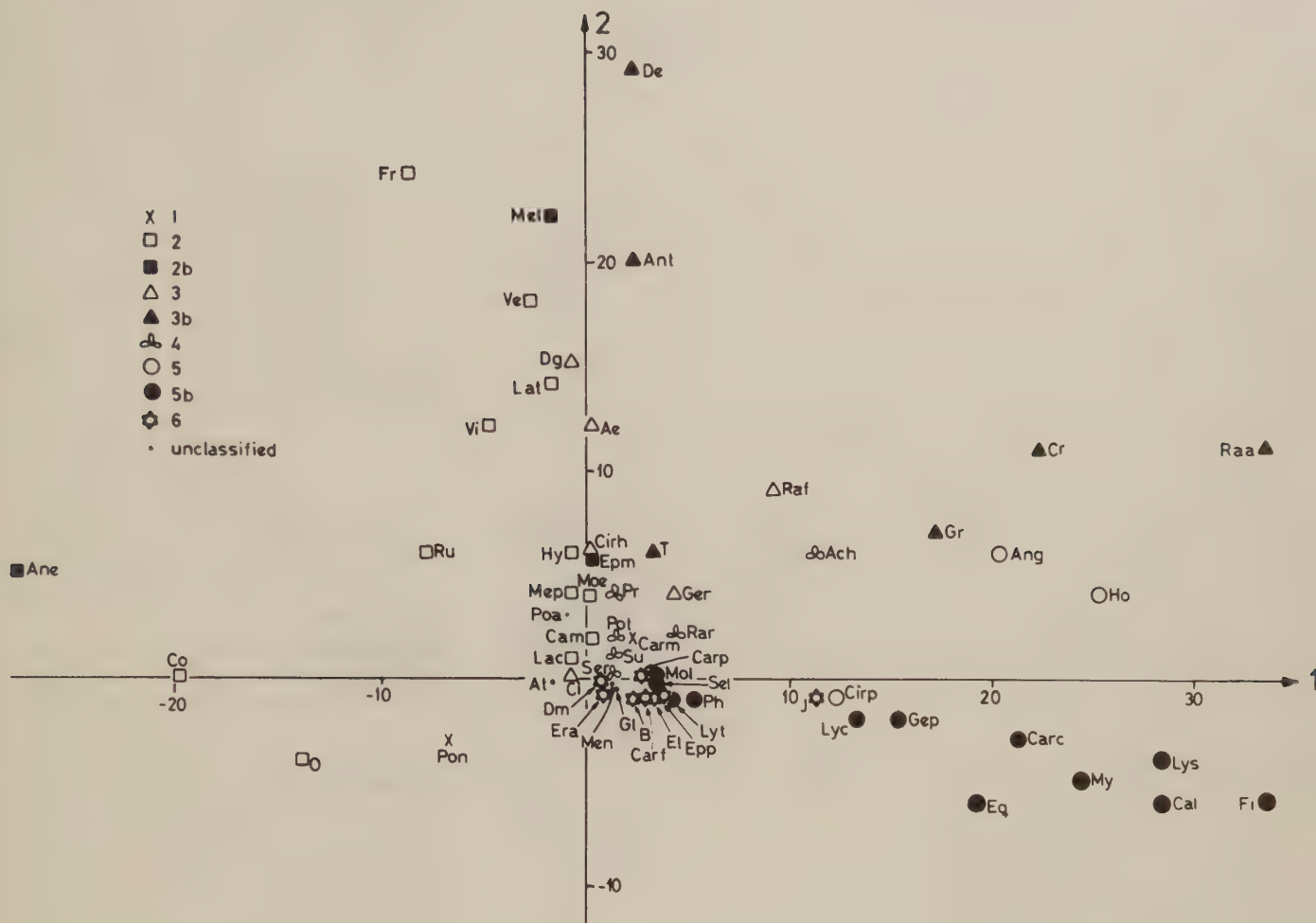
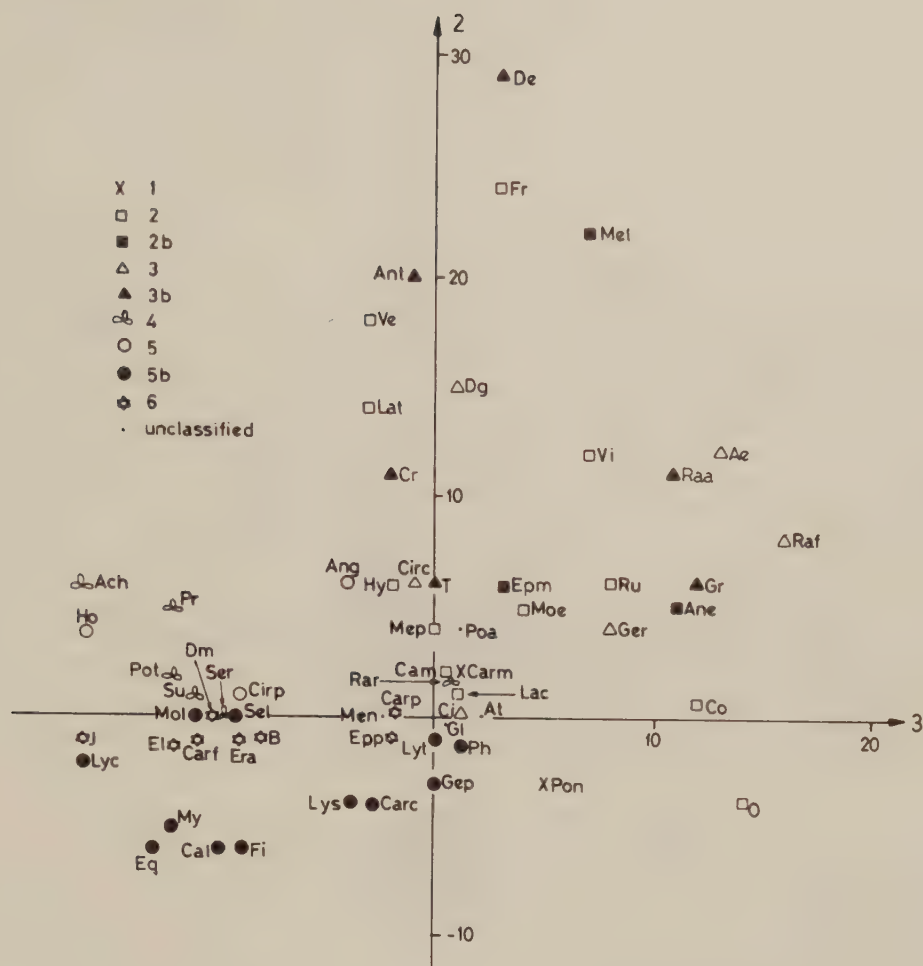


Fig. 1. Presence of species and ecological groups on soil-water regimes. The ecological groups are further discussed in Andersson 1970.



Achillea ptarmica	Ach.	Convallaria majalis	Co.	Glyceria fluitans	Gl.	Oxalis acetosella	O.
Aegopodium podagraria	Ae.	Crepis paludosa	Cr.	Holcus lanatus	Ho.	Phalaris arundinacea	Ph.
Anemone nemorosa	Ane.	Dactylis glomerata	Dg.	Hypericum perforatum	Hy.	Poa annua	Poa.
Angelica sylvestris	Ang.	Dactylorhiza majalis	Dm.	Juncus conglomeratus	J.	P. nemoralis	Pon.
Anthriscus sylvestris	Ant.	Deschampsia caespitosa	De.	Lactuca muralis	Lac.	Potentilla erecta	Pot.
Athyrium filix-femina	At.	Eleocharis uniglumis	El.	Lathyrus montanus	Lat.	Prunella vulgaris	Pr.
Briza media	B.	Epilobium montanum	Epm.	Lychnis flos-cuculi	Lyc.	Ranunculus auricomus	Raa.
Caltha palustris	Cal.	E. parviflorum	Epp.	Lyminachia vulgaris	Lys.	R. ficaria	Raf.
Campanula trachelium	Cam.	Equisetum arvense	Eq.	Lythrum salicaria	Lyt.	R. repens	Rar.
Carex caespitosa	Carc.	Eriophorum angustifolium	Era.	Melampyrum pratense	Mep.	Rubus saxatilis	Ru.
C. flacca	Carf.	Filipendula ulmaria	Fi.	Melandrium rubrum	Mel.	Selinum carvifolia	Sel.
C. montana	Carm.	Fragaria vesca	Fr.	Mentha sp.	Men.	Serratula tinctoria	Ser.
C. panicea	Carp.	Geranium palustre	Gep.	Moehringia trinervia	Moe.	Succisa pratensis	Su.
Circaea lutetiana	Ci.	G. robertianum	Ger.	Molinea coerulea	Mol.	Trollius europaeus	T.
Circium heterophyllum	Cirh.	Geum rivale	Gr.	Myosotis palustris	My.	Veronica chamaedrys	Ve.
C. palustre	Cirp.					Viola riviniana	Vi.

Fig. 2. Loadings of species on the first and second principal axes of PCA-ordination of the covariance matrix. The axes account for 33 and 13 % respectively of the total variance in the data ($n = 62$, $N = 97$). Ecological groups of species according to Fig. 1 are indicated.



Achillea ptarmica	Ach.	Convallaria majalis	Co.	Glyceria fluitans	Gl.	Oxalis acetosella	O.
Aegopodium podagraria	Ae.	Crepis paludosa	Cr.	Holcus lanatus	Ho.	Phalaris arundinacea	Ph.
Anemone nemorosa	Ane.	Dactylis glomerata	Dg.	Hypericum perforatum	Hy.	Poa annua	Poa.
Angelica sylvestris	Ang.	Dactylorhiza majalis	Dm.	Juncus conglomeratus	J.	P. nemoralis	Pon.
Anthriscus sylvestris	Ant.	Deschampsia caespitosa	De.	Lactuca muralis	Lac.	Potentilla erecta	Pot.
Athyrium filix-femina	At.	Eleocharis uniglumis	El.	Lathyrus montanus	Lat.	Prunella vulgaris	Pr.
Briza media	B.	Epilobium montanum	Epm.	Lychnis flos-cuculi	Lyc.	Ranunculus auricomus	Raa.
Caltha palustris	Cal.	E. parviflorum	Epp.	Lysimachia vulgaris	Lys.	R. ficaria	Raf.
Campanula trachelium	Cam.	Equisetum arvense	Eq.	Lythrum salicaria	Lyt.	R. repens	Rar.
Carex caespitosa	Carc.	Eriophorum angustifolium	Era.	Melampyrum pratense	Mep.	Rubus saxatilis	Ru.
C. flacca	Carf.	Filipendula ulmaria	Fi.	Melandrium rubrum	Mel.	Selinum carvifolia	Sel.
C. montana	Carm.	Fragaria vesca	Fr.	Mentha sp.	Men.	Serratula tinctoria	Ser.
C. panicea	Carp.	Geranium palustre	Gep.	Moehringia trinervia	Moe.	Succisa pratensis	Su.
Circaea lutetiana	Ci.	G. robertianum	Ger.	Molinia coerulea	Mol.	Trollius europaeus	T.
Circium heterophyllum	Cirp.	Geum rivale	Gr.	Myosotis palustris	My.	Veronica chamaedrys	Ve.
C. palustre	Cirp.					Viola riviniana	Vi.

Fig. 3. Loadings of species on the second and third principal axes of PCA-ordination of the covariance matrix. The axes account for 13 and 11 % respectively of the total variance in the data ($n = 62$, $N = 97$). Ecological groups of species according to Fig. 1 are indicated.



Achillea ptarmica	Ach.	Convallaria majalis	Co.	Glyceria fluitans	Gl.	Oxalis acetosella	O.
Aegopodium podagraria	Ae.	Crepis paludosa	Cr.	Holcus lanatus	Ho.	Phalaris arundinacea	Ph.
Anemone nemorosa	Ane.	Dactylis glomerata	Dg.	Hypericum perforatum	Hy.	Poa annua	Poa.
Angelica sylvestris	Ang.	Dactylorhiza majalis	Dm.	Juncus conglomeratus	J.	P. nemoralis	Pon.
Anthriscus sylvestris	Ant.	Deschampsia caespitosa	De.	Lactuca muralis	Lac.	Potentilla erecta	Pot.
Athyrium filix-femina	At.	Eleocharis uniglumis	El.	Lathyrus montanus	Lat.	Prunella vulgaris	Pr.
Briza media	B.	Epilobium montanum	Epm.	Lychnis flos-cuculi	Lyc.	Ranunculus auricomus	Raa.
Caltha palustris	Cal.	E. parviflorum	Epp.	Lysimachia vulgaris	Lys.	R. ficaria	Raf.
Campanula trachelium	Cam.	Equisetum arvense	Eq.	Lythrum salicaria	Lyt.	R. repens	Rar.
Carex caespitosa	Carc.	Eriophorum angustifolium	Era.	Melampyrum pratense	Mep.	Rubus saxatilis	Ru.
C. flacca	Carf.	Filipendula ulmaria	Fi.	Melandrium rubrum	Mel.	Selinum carvifolia	Sel.
C. montana	Carm.	Fragaria vesca	Fr.	Mentha sp.	Men.	Serratula tinctoria	Ser.
C. panicea	Carp.	Geranium palustre	Gep.	Moehringia trinervia	Moe.	Succisa pratensis	Su.
Circaea lutetiana	Ci.	G. robertianum	Ger.	Molinia coerulea	Mol.	Trollius europaeus	T.
Cirsium heterophyllum	Cirh.	Geum rivale	Gr.	Myosotis palustris	My.	Veronica chamaedrys	Ve.
C. palustre	Cirp.					Viola riviniana	Vi.

Fig. 4. Loadings of species on the first and third principal axes of PCA-ordination of the covariance matrix. The axes account for 33 and 11 % respectively of the total variance in the data ($n = 62$, $N = 97$). Ecological groups of species according to Fig. 1 are indicated.

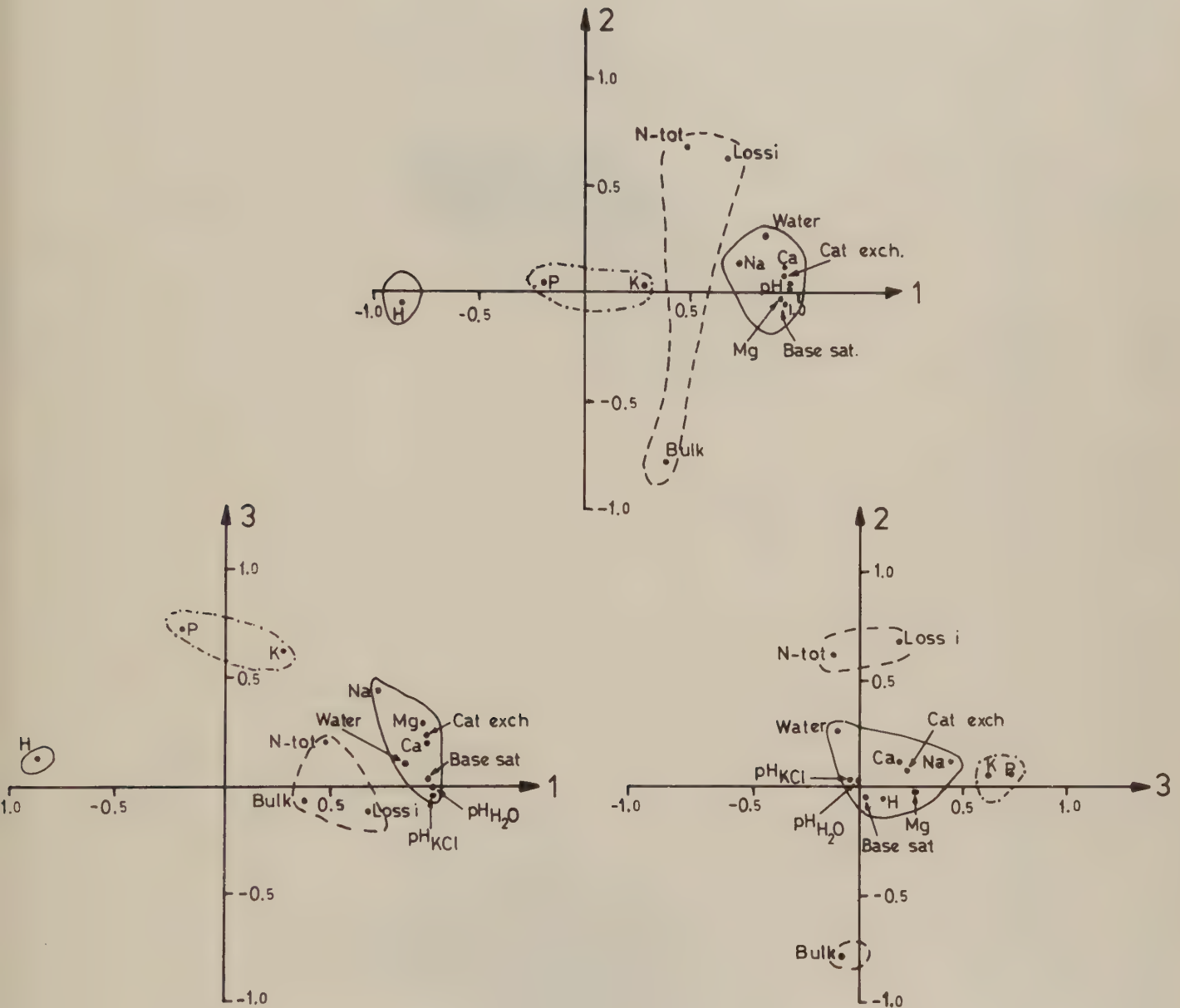


Fig. 5. Loadings of environmental variables on the first, second and third principal axes of PCA-ordination of the correlation matrix. The axes account for 62, 11 and 8% respectively of the total variance in the data ($n = 14$, $N = 97$). The isolines drawn indicate the A- and B-variables, see p 7. Abbreviations of variables given in section 3.2.1.2.

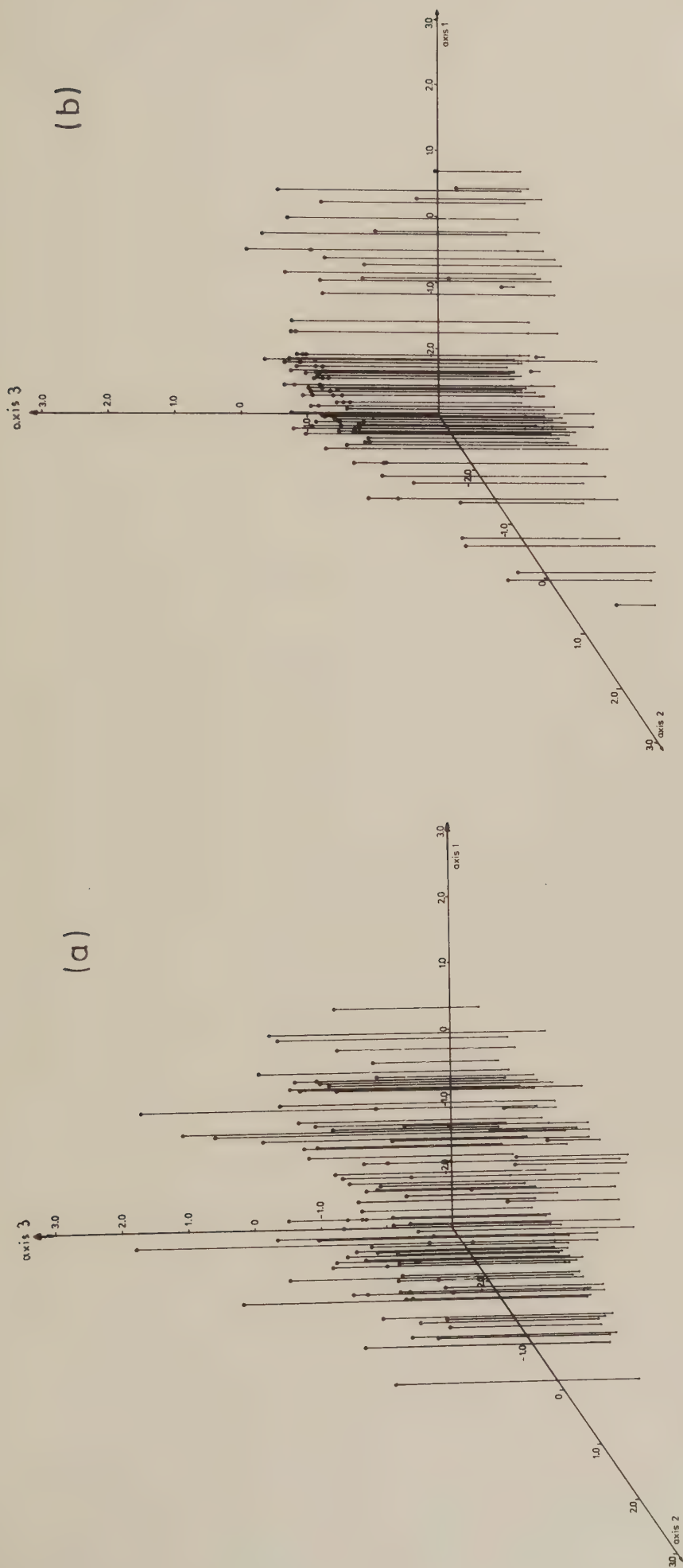


Fig. 6a. Stand scores on the first, second and third principal vegetation axes of PCA-ordination of the covariance matrix ($n = 62$, $N = 97$). Variance as in Figs. 2, 3 and 4.

Fig. 6b. Stand scores on the first, second and third principal environment axes of PCA-ordination of the correlation matrix ($n = 14$, $N = 97$). Variance as in Table 4 and Fig. 5.

